Differential predation by the generalist predator *Orius insidiosus* on congeneric species of thrips that vary in size and behavior

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Abstract

We investigated interactions between the generalist predator *Orius insidiosus* (Say) (Heteroptera: Anthocoridae) and two species of thrips prey, *Frankliniella bispinosa* (Morgan) and *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae), and interspecific differences in morphology and behavior between these prey species that could contribute to differences in predation by *O. insidiosus*. *Frankliniella occidentalis* is significantly larger than *F. bispinosa*. *Frankliniella bispinosa* has greater mobility compared with *F. occidentalis*. When *O. insidiosus* was offered either *F. bispinosa* or *F. occidentalis* as prey in single species trials, there were no significant differences in the number of prey captured. However, *O. insidiosus* had significantly more encounters with *F. bispinosa* than with *F. occidentalis*. In arenas with equal numbers of both species, *O. insidiosus* encountered and captured *F. occidentalis* more than *F. bispinosa*. In large arenas with two pepper plants (*Capsicum annuum* L.), *O. insidiosus* preyed on more *F. occidentalis* than on *F. bispinosa*. These results indicate that *O. insidiosus* can prey on both thrips species, but that it preferentially captures *F. occidentalis*. The greater locomotion and movement of *F. bispinosa*, perhaps combined with its smaller size, allow it to evade predation by *O. insidiosus* better than *F. occidentalis*. Consequently, the observed preference of *O. insidiosus* for *F. occidentalis* is not exclusively a function of active selection by the predator but also could arise from inherent differences among prey. We propose this differential predation as a mechanism contributing to observed differences in the temporal dynamics of these species in pepper fields.

Introduction

Generalist predators can forage on a broad spectrum of prey, yet they may show distinct preferences for particular prey. Thus, generalist predators may capture and consume prey in amounts disproportionate to the overall abundance of potential prey in the environment (Chesson, 1983). Such predation preferences can produce significantly different population dynamics in closely related species of prey and consequently alter community composition (McPeek, 1990; Settle & Wilson, 1990; Gascon, 1992; Blaustein, 1998).

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Although prey preference implies a predator-based process, the phenomenon of preference can be a function of two processes: active choice by the predator and passive selection by the prey (Pastorok, 1981). These components need not be mutually exclusive, but rather may jointly influence differential predation (Blais & Maly, 1993). Active choice occurs when predators discriminate among prey of different quality (Williams, 1987; Lang & Gsödl, 2001). Active selection factors that can influence predation include size variation among available prey types (O'Brien et al., 1976; Peckarsky, 1980) and differential nutritional quality of various prey to a predator (Eubanks & Denno, 2000; Roger et al., 2000; Mendes et al., 2002).

Passive selection is based on intrinsic differences among prey types wherein the prey affects the outcome of encounters

with predators (Riessen et al., 1984; McPeek, 1990; Dyer & Floyd, 1993). Vulnerability of prey when encountered by a predator can drive differential predation, whereby certain prey are better able than others to evade or deter predators (Barbeau & Scheibling, 1994; Walls, 1995; Lang & Gsödl, 2001). This factor may be critically important when predators encounter prey that are morphologically similar yet differ in their behavior.

Here, we examine predation by *Orius insidiosus* (Say) (Heteroptera: Anthocoridae) on two congeneric species of flower thrips that are common in Florida and the southeastern USA, *Frankliniella bispinosa* (Morgan) and *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae). *Frankliniella occidentalis* is a cosmopolitan pest (Kirk, 2002) that was recorded first in Florida in the mid-1980s (Olson & Funderburk, 1986), whereas *F. bispinosa* is endemic to Florida and surrounding regions of the southeastern USA. Both species are highly polyphagous (Chellemi et al., 1994) and cause significant damage to a variety of crops through their feeding and oviposition (Olson & Funderburk, 1986; Childers et al., 1990; Childers & Achor, 1991) and as vectors of tomato spotted wilt virus (Ullman et al., 1997; Webb et al., 1997; Avila, 2004). In the field, adults and larvae of these species occur almost exclusively in flowers as opposed to other plant structures (Hansen et al., 2003).

Orius insidiosus is a key natural enemy of *Frankliniella* species (Sabelis & van Rijn, 1997). In the southern USA, *O. insidiosus* is a significant factor in the predictable seasonal declines in *Frankliniella* spp. that follow population peaks, which occur in the spring, and it is able to suppress *Frankliniella* spp. populations in field-grown pepper (*Capsicum annuum* L.) (Funderburk et al., 2000; Ramachandran et al., 2001; Reitz et al., 2003). However, these studies also have shown that *F. bispinosa* populations tend to persist longer in the growing season than those of *F. occidentalis*, which suggests that *O. insidiosus* selectively preys on *F. occidentalis*.

Understanding interactions that occur between the predator *O. insidiosus* and its thrips prey can provide important insights into thrips dynamics at larger ecological scales and a better understanding of how to manage pest thrips. Therefore, we performed a series of experiments to assess how predation by *O. insidiosus* may be affected by interspecific differences between *F. bispinosa* and *F. occidentalis*. To determine how these closely related thrips species may differ, we compared their relative body size and behavioral time budgets. To determine if *O. insidiosus* interacts differently with these species, we examined predation in single species arenas and in small and large-scale arenas with mixed species.

Materials and methods

Experimental insects

Frankliniella bispinosa and *F. occidentalis* were collected from cultivated and uncultivated host plants in Alachua and Gadsden counties, FL, USA, to establish colonies for use in assays. Thrips were supplied with bean pods (*Phaseolus vulgaris* L.) as a food and oviposition substrate. Bean pods were lightly streaked with honey, and bee pollen was added to containers as a dietary supplement (Tsai et al., 1996). All colonies were maintained in environmental chambers, with a L14:D10 photoperiod and 70–80% r.h.

Orius insidiosus was collected from pepper and crape myrtle (*Lagerstroemia indica* L.) in Gadsden, Alachua, and Marion counties, FL, USA, and maintained under conditions similar to those used for rearing thrips. Bean pods were provided as an oviposition substrate. Prey for *O. insidiosus* consisted of both *Frankliniella* species, with *Helicoverpa zea* (Boddie) (Lepidoptera: Noctuidae) eggs and bee pollen used as dietary supplements. Three- to 5-day-old F_1 generation adults from field collected *O. insidiosus* were used in experiments. Predators were held individually in containers with a bean pod but no prey or pollen for 12–16 h before use in assays.

Relative size of *Frankliniella bispinosa* and *Frankliniella occidentalis*

To determine if differences in size of *F. occidentalis* and *F. bispinosa* might affect predation by *O. insidiosus*, we compared the relative sizes of adult females and males of each species. Specimens were placed in physiological saline on a slide, oriented dorsum up, and a digital picture of each was taken with a Nikon 950 camera (Nikon, Tokyo, Japan) mounted on a stereomicroscope (63 × magnification). Size was estimated by measuring the dorsal area of the head, thorax, and abdomen of each, using SIGMASCAN 5.0 image analysis software (SPSS, Chicago, IL, USA). These body size measurements were analyzed by a two-way analysis of variance (ANOVA).

Activity budgets of *Frankliniella bispinosa* and *Frankliniella occidentalis*

Activity budgets were determined following the protocols of Hansen et al. (2003). Individual adult females were placed into a Petri dish (100 mm diameter × 15 mm depth) between one leaf, one flower bud, and one open flower blossom of 'Camelot X3R' pepper. Plant parts were excised immediately before use from greenhouse-grown plants. Individual thrips were observed under a videomicroscope at 40 × magnification for 1 h (n = 18 for *F. occidentalis*, n = 21 for *F. bispinosa*). The time spent on different behaviors and the location of events were

recorded (OBSERVER version 4.0, Noldus Information Technology, Sterling, VA, USA). Behaviors were categorized as feeding, resting, or locomotion, with locations being on flower, bud, or leaf, or off plant parts. A feeding session occurred when an individual stood still with its forelegs apart, antennae still, usually nodding its head up and down, as it probed with its mandible. Locomotion included walking and flying. Resting included when a thrips was quiescent or grooming. Rarely observed behaviors (e.g., oviposition) were combined with 'resting' for data analysis.

Time spent on each behavior and location was converted to a proportion of the total observation time. A multivariate analysis of variance (MANOVA) was used to compare the time budgets of *F. bispinosa* and *F. occidentalis* (Cisneros & Rosenheim, 1998). Data were transformed $\ln[(\% \text{ time spent on a category} + 1)/(100 - \% \text{ time spent on same category} + 1)]$ to satisfy the assumption of normality and the unit sum constraint (Neter et al., 1996). Because we were specifically interested in determining if thrips species differed in amounts of locomotion and feeding, least squares means comparisons were performed on those data (least squares means option; SAS, 1999). Back transformed means and their 95% confidence intervals are presented (Sokal & Rohlf, 1995).

Predation in single species arenas

Predation arenas were constructed from polystyrene Petri dishes (100 mm diameter × 15 mm depth) and lids, which had three screen-covered holes (1 cm diameter) for ventilation and a capped entrance hole to introduce insects. For each replicate, the petiole of a single, fully expanded pepper flower ('Camelot X3R') was cut near its base, and the petiole of the flower was placed into a small water-filled tube glued to the base of the dish. Female thrips were aspirated from the appropriate colonies, chilled for 1 min to facilitate handling, and then introduced onto the flower. Thrips were allowed to acclimate for 1 h before predator introduction. Predators were placed on a small platform that was attached to the flower holder by a straight pin. Arenas were placed individually under a stereomicroscope (50 × magnification) and illuminated with a fiber optic light for behavioral observations.

We tested three densities of thrips: 5, 10, and 20 thrips per arena, with both male and female *O. insidiosus*. For each replicate, a single *O. insidiosus* was introduced into the arena, and behaviors were recorded for 1 h, which based on preliminary observations would allow *O. insidiosus* to capture and consume several prey and thus express any potential predation differences. Recording commenced once the predator left the landing site and began

walking on the pin toward the flower. The number of encounters *O. insidiosus* had with thrips, the number of thrips captured by *O. insidiosus*, the amount of time *O. insidiosus* spent capturing and subduing prey, and the amount of time *O. insidiosus* spent feeding on prey were recorded. These times were combined to determine total handling time. We defined an encounter as directed movements by *O. insidiosus* toward an individual thrips. Each encounter resulted in either the capture or escape of the target thrips.

Fifteen replicates of each predator sex, prey species, and prey density combination were conducted, and data were analyzed by a three-factor analysis of variance (ANOVA). All data were checked for normality and homoscedasticity. The numbers of encounters and captures were transformed by $\sqrt{(y + 0.375)}$ before analysis. Means were separated by least squares means t-tests, based on the Bonferroni corrected P-values given in the results. Means and their standard errors are presented.

Predation in mixed species arenas

The same type of arena and procedures as described for the single prey species test were used, except that a mixture of both *F. occidentalis* and *F. bispinosa* females were used, with an intermediate density of 10 thrips (five *F. bispinosa* : five *F. occidentalis*) per arena. We conducted tests with both male and female *O. insidiosus*.

For each trial, we recorded the number of encounters, captures, and handling time for successful captures by *O. insidiosus*. The species of thrips in each encounter and capture was recorded. For each replicate, a single *O. insidiosus* was introduced into the arena, and behaviors were recorded for 1 h, with recording commencing once the predator left the landing site and began walking on the pin toward the flower.

We analyzed the data in two ways. First, we used ANOVA to test if the total numbers of encounters or captures differed between predator sexes (PROC GLM, SAS, 1999). Second, we fitted data on differences in these dependent variables between prey species to an ANOVA with predator sex as a main effect and used least squares means t-tests to test if mean differences in encounters, captures, or handling times for each predator sex were significantly different from zero. Differences for dependent variables were calculated as *F. bispinosa* minus *F. occidentalis* for each replicate arena; therefore, negative values reflect greater values for *F. occidentalis* than for *F. bispinosa*. Data were checked for normality and homoscedasticity, and did not need transformation. For multiple mean comparisons, significance was determined based on the Bonferroni corrected P-values that are given in the results.

Predation in mixed species arenas with whole plants

Pots containing two pepper plants ('Camelot X3R') of approximately the same size, each with a single open flower at approximately the same height, were used in these trials. A Plexiglas cylinder (15.5 cm in diameter × 36 cm in height) was placed over the plants, and the base of the cylinder was pushed into the soil to prevent insects from escaping. Cylinder tops were covered with thrips-proof screen. A hole (1 cm diameter), placed 10 cm from the top and covered with a rubber stopper, was used as an entrance for predator introduction.

We tested four densities of thrips, with equal numbers of female *F. bispinosa* and *F. occidentalis* in each replicate. The densities tested were 10 total thrips per arena, 20 per arena, 40 per arena, and 80 per arena. One-half of the replicates at each density were experimental trials with *O. insidiosus*, and the other half of the replicates were control trials without *O. insidiosus*. Thirteen replicates were conducted for each of the predator and density treatments. For each replicate, a vial containing the thrips was placed directly under and touching one of the plants, and the thrips were allowed to move out of the vial onto the plant. In the predator trials, a single adult female *O. insidiosus* was introduced 4 h after the thrips were released. Twenty-eight hours after the introduction of the thrips (i.e., 24 h after predator introduction), the plants were destructively sampled to determine the number of surviving thrips.

From these data, we were able to compare the inherent survivorship of both thrips species on pepper and the impact of predation by *O. insidiosus*. The control cages were used to compare the inherent survivorship of *F. bispinosa* and *F. occidentalis* on pepper in the absence of *O. insidiosus*. Next, we compared numbers of surviving thrips of each species between control cages and the experimental cages with *O. insidiosus* to reflect predation inflicted by *O. insidiosus* on each species (Clements & Yeargan, 1997). Then we examined the differences between numbers of *F. occidentalis* and *F. bispinosa* surviving in the experimental treatments to estimate the extent of differential predation.

We conducted two-factor ANOVA on the number of surviving *F. bispinosa*, *F. occidentalis*, and their difference within replicates, using prey density and *O. insidiosus* treatments as factors. Specific comparisons were made using least squares means t-tests, with significance based on the Bonferroni corrected P-values that are given in the results. Because there was no expectation of one species surviving better than the other species, we conducted two-tailed tests to test for interspecific differences in survivorship in the respective treatments. Because we hypothesized that numbers of surviving thrips would be lower in the presence of the predator *O. insidiosus* than in its absence,
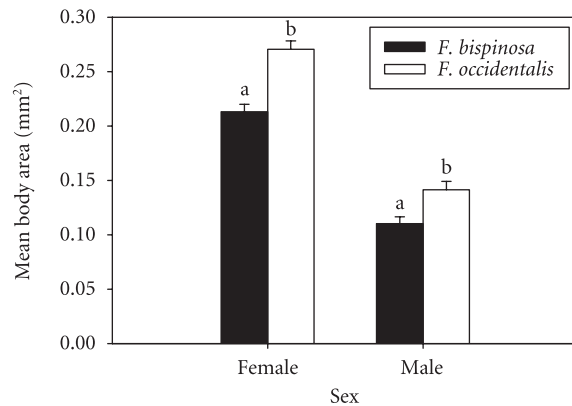
Figure 1 Body size comparisons of adult females and males of *Frankliniella bispinosa* (n = 12, 7, respectively) and *Frankliniella occidentalis* (n = 10, 9, respectively). Data are the area of the dorsum of the head, thorax, and abdomen (mean + SEM). For each sex, different letters above bars indicate a significant difference between species (P<0.05).

we used one-tailed tests to compare numbers of each species surviving in the control and experimental treatments at each density.

Results

Relative size of *Frankliniella bispinosa* and *Frankliniella occidentalis*

The interaction between species and sex for size was not significant ($F_{1,33} = 0.01$, P = 0.94), indicating that interspecific size differences were consistent between the sexes. *Frankliniella occidentalis* was significantly larger than *F. bispinosa* ($F_{1,33} = 33.98$, P<0.0001; Figure 1). Female *F. occidentalis* were approximately 27% larger than female *F. bispinosa*, and male *F. occidentalis* were approximately 28% larger than male *F. bispinosa*. Females of both species were nearly twice the size of males ($F_{1,33} = 249.53$, P<0.0001; Figure 1).

Activity budgets of *Frankliniella bispinosa* and *Frankliniella occidentalis*

The overall activity budgets of *F. bispinosa* and *F. occidentalis* were significantly different (Wilks' λ = 0.663: $F_{2,36} = 9.17$, P = 0.0006; Figure 2). *Frankliniella bispinosa* was significantly more active than *F. occidentalis* (t = 2.09, P = 0.043), spending approximately 2.4-fold as much time moving as *F. occidentalis*. In contrast, *F. occidentalis* spent approximately three-fold more time feeding on pepper than did *F. bispinosa* (t = 4.20, P = 0.0002). Both species showed a high affinity for flowers as opposed to foliage or flower buds. Of the time spent on plant parts, over 90% for each species was spent on the flower. Almost 100% of feeding activity for both species occurred in the flowers.
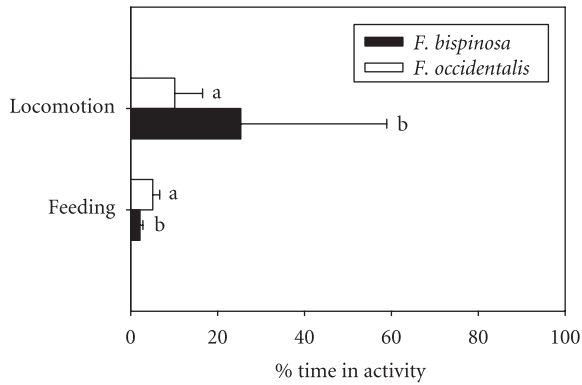
Figure 2 Percent time spent engaged in locomotion and feeding by adult females of *Frankliniella bispinosa* and *Frankliniella occidentalis* on pepper plant parts in laboratory choice experiments. Back-transformed means and 95% confidence intervals are shown. For each activity, different letters on the right side of the bars indicate a significant difference between species (P<0.05).

Predation in single species arenas

Both female and male *O. insidiosus* had significantly more encounters with *F. bispinosa* than they did with *F. occidentalis* ($F_{1,168}$ = 10.59, P = 0.0014; Figure 3). There was a significant difference between the sexes of *O. insidiosus*, with females having significantly more encounters with prey than *O. insidiosus* males ($F_{1,168}$ = 12.42, P = 0.0005). There was a significant sex*density interaction ($F_{2,168}$ = 3.46, P = 0.0337). The number of encounters that female *O. insidiosus* had with prey was not related to prey density (P>0.05, least squares means t-tests; Figure 3A); however, males had significantly more encounters with prey at the highest density of 20 thrips per arena than at the lower densities of 5 or 10 thrips per arena (P<0.018, least squares means t-tests; Figure 3A).

Although *O. insidiosus* made greater numbers of encounters with *F. bispinosa* than with *F. occidentalis*, *F. bispinosa* was better able to escape from these encounters than was
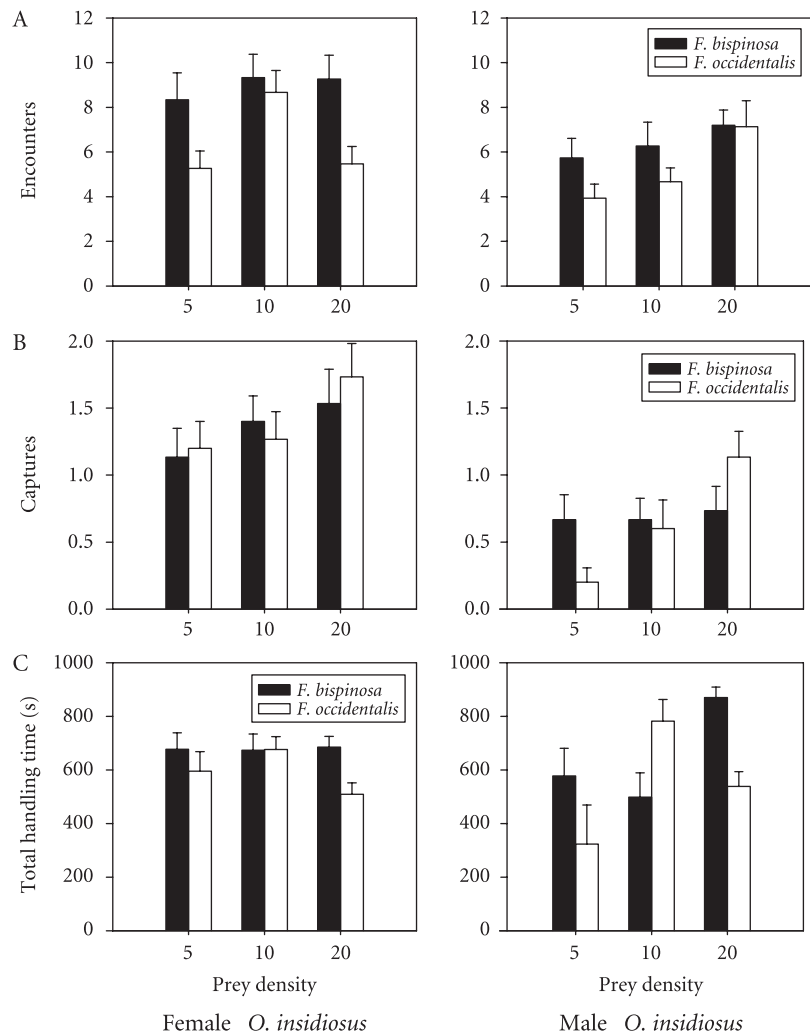
Figure 3 Mean (+ SEM) number of (A) encounters, (B) captures, and (C) total handling time for captures that female and male *Orius insidiosus* had when preying upon either *Frankliniella bispinosa* or *Frankliniella occidentalis* adults in single species prey trials at three different densities of thrips. Total handling time consists of time to capture and subdue prey and feeding time. *Orius insidiosus* had significantly more encounters with *F. bispinosa* than with *F. occidentalis*. There was no significant difference in captures of *F. bispinosa* and *F. occidentalis*. Handling time was significantly longer for *F. bispinosa* than for *F. occidentalis*.
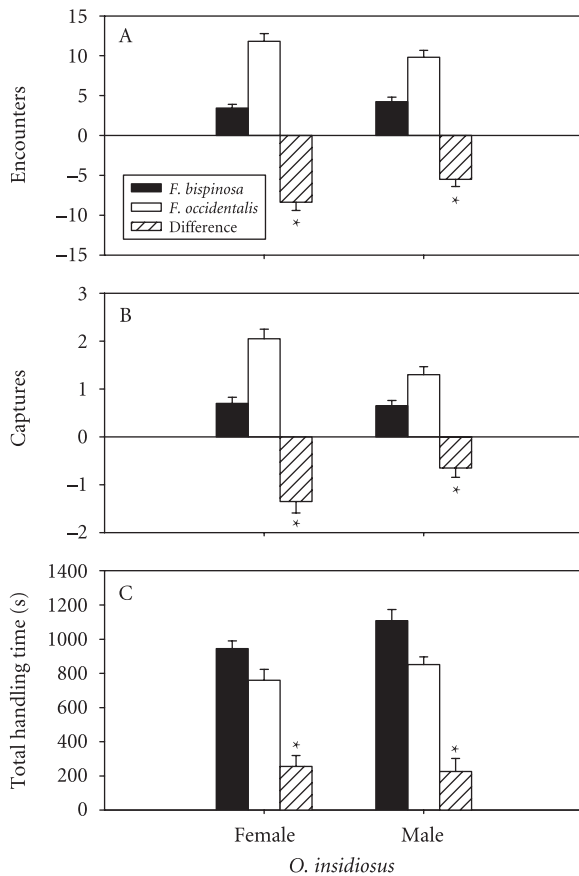
Figure 4 Mean (+ SEM) numbers of (A) encounters, (B) captures, and (C) total handling time for captures that female and male *Orius insidiosus* had with *Frankliniella bispinosa* or *Frankliniella occidentalis* adults in mixed prey species trials. Total handling time consists of time to capture and subdue prey and feeding time. Mean (+ SEM) differences between prey species for each variable are also shown. Differences are calculated as *F. bispinosa* – *F. occidentalis*. Therefore, negative values for the differences indicate that quantities for *F. occidentalis* are greater than for *F. bispinosa*. Asterisks (*) indicate mean differences that are significantly different from zero (P<0.05).

F. occidentalis ($F_{1,168} = 11.26$, P = 0.001). Ultimately, although *O. insidiosus* was less successful in captures per encounter against *F. bispinosa*, there was no difference in the numbers of captures of the two prey species ($F_{1,168} = 0.03$, P = 0.86; Figure 3B). The number of captures was significantly higher with 20 thrips per arena than at the two lower densities of 5 and 10 thrips per arena ($F_{2,168} = 5.32$, P = 0.0057). As with the numbers of encounters, there was a significant difference in captures between the predator sexes, with females capturing significantly more prey than males ($F_{1,168} = 35.07$, P<0.0001).

Most of the handling time was spent in feeding on prey. The mean time for a capture to occur was 1.5 ± 0.07 s from

the initiation of an encounter until a prey was subdued. Although *F. occidentalis* is larger than *F. bispinosa*, *O. insidiosus* spent significantly more time feeding on *F. bispinosa* (722 ± 29.7 s) than on *F. occidentalis* (618 ± 35.5 s; $F_{1,78} = 6.24$, P = 0.0146, for trials in which feeding was completed before the end of the observation session; Figure 3C). *Orius insidiosus* removed virtually all of the extractable food from their prey, leaving just the sclerotized exoskeleton and tissue of the thrips.

Predation in mixed species arenas

When *O. insidiosus* was in arenas with both *F. bispinosa* and *F. occidentalis*, both female and male predators, had significantly more encounters with *F. occidentalis* than with *F. bispinosa* (least squares means t-test for mean difference = 0: females: t = −8.12, P<0.0001; males: t = −6.15, P<0.0001; Figure 4A); yet there was no difference in the total numbers of encounters for the two sexes ($F_{1,38} = 0.54$, P = 0.46).

Although female *O. insidiosus* had greater numbers of captures than males ($F_{1,38} = 7.01$, P = 0.012), both sexes had significantly more captures of *F. occidentalis* than of *F. bispinosa* (least squares means t-test for mean difference = 0: females: t = −5.54, P<0.0001; males: t = −3.32, P = 0.011; Figure 4B). As was the case in the no-choice trials, feeding comprised almost all of the handling time, and both female and male *O. insidiosus* had significantly longer mean feeding times for *F. bispinosa* than for *F. occidentalis* ($F_{1,23} = 23.63$, P<0.0001). This difference in feeding times between prey species was consistent between the sexes of *O. insidiosus* (predator sex*prey species interaction: $F_{1,23} = 0.10$, P = 0.758; Figure 4C), yet male *O. insidiosus* had longer feeding times per prey item (822 ± 61 s) than females (562 ± 59 s; $F_{1,23} = 9.47$, P = 0.0053).

Predation in mixed species arenas with whole plants

Overall, there was a significant density*predator treatment interaction for differences between surviving *F. bispinosa* and *F. occidentalis* in the whole plant trials ($F_{3,96} = 4.28$, P = 0.007; Figure 5). This interaction indicates that differences in species survival varied in accordance with both density-dependent factors and predation. Because of this significant interaction, we analyzed differences between prey species separately for each density and predator treatment combination. In treatments without *O. insidiosus*, there were no significant differences in survival of *F. bispinosa* and *F. occidentalis* at the two lowest densities of 10 and 20 total thrips per arena (P>0.05 for least squares means t-tests that mean differences between species = 0); yet, at the higher densities of 40 and 80 thrips per arena, significantly more *F. occidentalis* survived than *F. bispinosa* (P = 0.0128 and 0.0262, respectively). However, at each
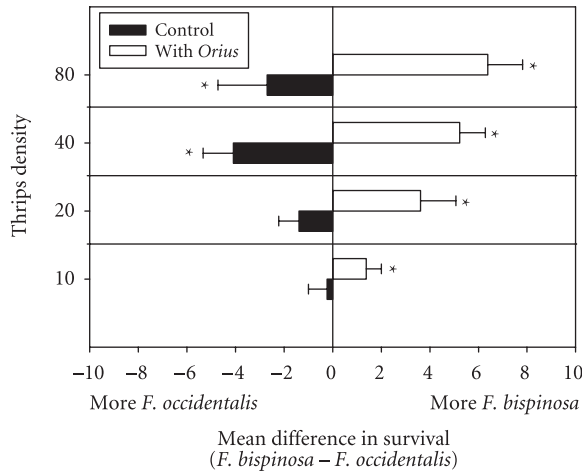
Figure 5 Mean differences (+ SEM) in numbers of surviving *Frankliniella bispinosa* and *Frankliniella occidentalis* in whole plant arenas at each of four densities, with or without *Orius insidiosus* present. Differences are calculated as *F. bispinosa – F. occidentalis*. Therefore, negative values for the differences indicate that quantities for *F. occidentalis* are greater than for *F. bispinosa*. Asterisks (*) indicate mean differences that are significantly different from zero (P<0.05).

density with *O. insidiosus* present, significantly more *F. bispinosa* than *F. occidentalis* survived (P<0.0392 for least squares means t-tests that mean differences between species = 0; Figure 5).

To determine if predation was a significant factor for either prey species, we compared numbers of survivors between control and experimental treatments, with the expectation that thrips numbers with *O. insidiosus* present would be significantly lower than in the controls. At each

density, there were significantly fewer *F. occidentalis* surviving with *O. insidiosus* than without *O. insidiosus* (P<0.045 for least squares means t-tests that mean differences between predation treatments for each prey species = 0; Figure 6). In contrast to those differences indicating that significant numbers of *F. occidentalis* were preyed upon, we found that numbers of *F. bispinosa* surviving in trials with *O. insidiosus* present were not significantly lower than in trials without *O. insidiosus* (P>0.05; Figure 6). These results suggest that in these large arenas with alternate prey, *O. insidiosus* did not prey extensively on *F. bispinosa*.

Discussion

Our series of experiments demonstrate that *O. insidiosus* exhibits differential predation on adults of *F. bispinosa* and *F. occidentalis*, with greater predation occurring on the larger and more sedentary *F. occidentalis* in mixed prey situations. *Orius insidiosus* was able to prey to some extent on *F. bispinosa*, but *F. bispinosa* was better able to escape and avoid predation than *F. occidentalis*. While a number of studies have shown that heteropteran predators display prey preferences when offered widely divergent types of prey, such as sessile vs. mobile prey types, and/or taxonomically distant species (Foglar et al., 1990; Hazzard & Ferro, 1991; Cloutier & Johnson, 1993; Cisneros & Rosenheim, 1997; Eubanks & Denno, 2000), few studies have addressed preference of heteropteran predators for closely related species of prey, such as the congeneric species that we tested (but see Fritsche & Tamo, 2000; Meyling et al., 2003).

From an applied perspective, the presence of alternative prey can have positive or adverse effects on biological control

Figure 6 Numbers of surviving *Frankliniella bispinosa* and *Frankliniella occidentalis* (mean + SEM) in whole plant arenas at each of four densities and with or without *Orius insidiosus* present. The initial densities of thrips are shown in the upper right corner of each graph; note different scales for each. Equal proportions of *F. bispinosa* and *F. occidentalis* were used in all trials. Asterisks (*) indicate that significantly fewer thrips of a particular species survived in the presence of the predator *O. insidiosus* than in its absence (P<0.05); ns indicates non significant difference.
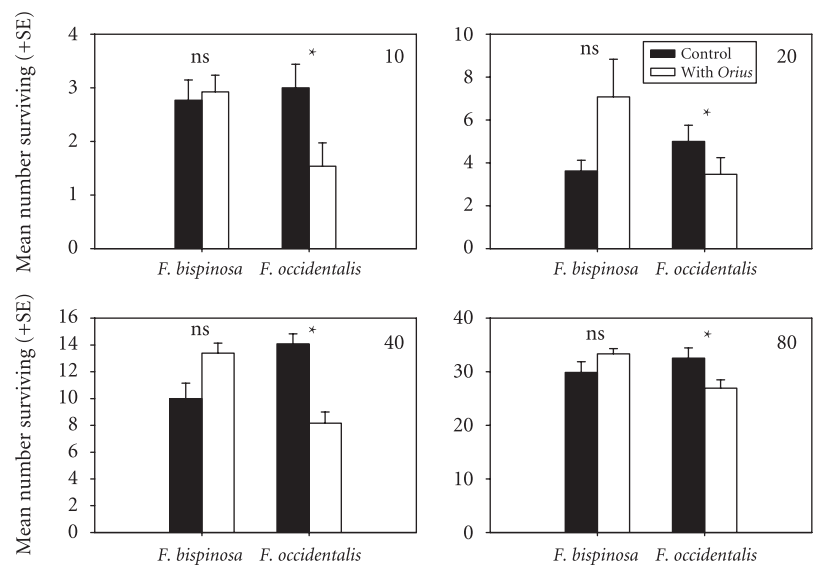
of a target species by a generalist predator, depending upon the different predator–prey interactions (Holt & Lawton, 1994; Symondson et al., 2002). Control can be enhanced if alternative prey allow the predator to persist when the target prey are scarce (Nomikou et al., 2002). In contrast, control can be compromised if alternative prey are more likely to be preyed upon than the target species (Honda & Luck, 1995; Koss & Snyder, 2005). Even with these findings, little emphasis has been placed on the effects of generalist predators in systems with multiple target pest species.

Because *F. occidentalis* and *F. bispinosa* are vectors of tomato spotted wilt virus, the management of both species is a key concern for vegetable growers. Parrella & Lewis (1997) proposed that natural enemies are not significant in regulating thrips populations in field crops; yet Funderburk et al. (2000) found that seasonal declines in abundances of *Frankliniella* spp. are closely correlated with increases in the abundance of *O. insidiosus*. Importantly though, populations of *F. occidentalis* tend to decline sooner than populations of *F. bispinosa*, which persist longer during the growing season (Ramachandran et al., 2001; Funderburk, 2002; Reitz et al., 2002). Field studies have shown that *F. bispinosa* moves among plants at a greater rate than *F. occidentalis* (Ramachandran et al., 2001; Reitz et al., 2003). This difference suggests that *F. occidentalis* is more sedentary than *F. bispinosa* and thus may be more vulnerable to predation (Sabelis & Van Rijn, 1997; Hansen et al., 2003; Baez et al., 2004).

Although similar numbers of *F. bispinosa* and *F. occidentalis* were captured in single prey species trials, predation by *O. insidiosus* did not operate in a frequency independent manner in the mixed species trials. Had *O. insidiosus* predation been frequency dependent, similar numbers of *F. occidentalis* and *F. bispinosa* should have been captured, as captures of one species would increase the probability of the alternate species being captured next. The selective predation on *F. occidentalis* remained consistent even as the likelihood of *O. insidiosus* encountering either species changed across the range of prey densities tested in the whole plant arenas.

The greater predation on *F. occidentalis* is consistent with *O. insidiosus* selectively preying on the larger, and thus likely, more nutritious prey. Various species of thrips, including *F. occidentalis*, have been shown to be intrinsically high quality prey for the development and reproduction of *Orius* spp. (Isenhour & Yeargan, 1981; Chyzik et al., 1995; Wearing & Colhoun, 1999; Fritsche & Tamo, 2000). Yet, we did not observe *O. insidiosus* rejecting any captured prey, which could be a mechanism to limit consumption of particular prey (Meyling et al., 2003). Therefore, the lower levels of predation that we observed for *O. insidiosus* on *F. bispinosa* in mixed species trials are not likely a result of

F. bispinosa being an inherently poor diet choice. In fact, *O. insidiosus* did not refuse to attack or capture *F. bispinosa* in mixed species arenas. The predators would engage any thrips in close proximity, but *F. bispinosa* was better able to escape encounters in single species trials predation, where the overall success rate (captures per encounter) of *O. insidiosus* was approximately 50% greater when offered *F. occidentalis* than when offered *F. bispinosa*, and *F. bispinosa* was less likely to be encountered in the mixed species trials. Consequently, *O. insidiosus* always captured significantly more *F. occidentalis* than *F. bispinosa* in mixed species arenas. In these trials, *O. insidiosus* encountered both prey species at various points throughout trials, indicating that predator satiation did not influence choice of prey, and selective preferences of the predator remained constant from the beginning to the end of the trials. Because *O. insidiosus* would readily attack either species it encountered, it appears that the more sedentary nature of *F. occidentalis* exposed them to more successful attacks from *O. insidiosus*. Therefore, the preference of *O. insidiosus* for *F. occidentalis* appears to be a result more of passive selection, based on vulnerability of the prey, rather than of active predator choice (Lang & Gsödl, 2001; Sukhanov & Omelko, 2002).

Inherent interspecific differences in behaviors, such as movement patterns, can be a key component in producing observed patterns of differential predation (Lawler, 1989). *Orius insidiosus* will prey more heavily on the less mobile larvae of *F. occidentalis* than on adults, but as abundance of larvae declines predation on adults increases (Baez et al., 2004). Fritsche & Tamo (2000) found that in single prey species arenas, *Orius albipennis* (Rueter) captured and consumed fewer *Megalurothrips sjostedti* (Trybom) than two other thrips prey species, *Ceratothripoides cameroni* (Priesner) and *Frankliniella schultzei* (Trybom). They attributed this difference to *M. sjostedti* being more active and better able to avoid predation than the other species. Meyling et al. (2003) suggest that the preference of *Anthocoris nemorum* (L.) and *Anthocoris nemoralis* (F.) for *Myzus persicae* Sulzer over *Macrosiphon euphorbiae* (Thomas) results from *M. euphorbiae* individuals being more likely than those of *M. persicae* to move when disturbed by a predator.

Differential predation can have significant consequences for population dynamics and biological control. The significant difference between the species in the whole plant control trials indicates that *F. occidentalis* has greater inherent survivorship than *F. bispinosa* on pepper. However, the presence of *O. insidiosus* reversed this difference, with the survivorship of *F. bispinosa* being much higher than that of *F. occidentalis*. Here, we show that prey preference of *O. insidiosus* is not exclusively a predator based phenomenon but also can arise from inherent differences

among prey. Regardless of the mechanism, *F. occidentalis* is more vulnerable than *F. bispinosa* to predation by *O. insidiosus*, and this differential predation may affect the temporal dynamics of these species. We propose that differential predation can be an important mechanism underlying the seasonal population dynamics of *F. occidentalis* and *F. bispinosa*, and other *Frankliniella* species observed in the southern USA.

Acknowledgements

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